J. N. Am. Benthol. Soc., 1989, 8(4):331-341

Discharge-export relationships in headwater streams: the influence of invertebrate manipulations and drought

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Abstract. The role of physical (discharge) and biological (macroinvertebrate communities) factors in the control of coarse (>4 mm) and fine (≤4 mm > 0.5 μm) particulate organic matter (FPOM) transport was studied in three headwater streams of the southern Appalachian Mountains. The role of discharge was determined by relating two years of continuous measurements obtained over discrete (ca. 2-wk) time intervals. The role of macroinvertebrates was examined by treating one of the three streams, C 54, with an insecticide during Year 2 to reduce populations and alter community structure.

Maximum discharge was the only discharge parameter which adequately predicted (linear regressions) FPOM export during a sampling interval ($r^2 \geq 0.70$). These regressions were unique for each stream and were constant between years for the untreated streams, despite a record drought during the second year. Relationships between discharge and export of coarse particulate organic matter (CPOM) were not as strong nor as consistent as those for FPOM. CPOM export was very sensitive to timing of CPOM inputs and storms (e.g., 78 to 88% of CPOM export during Year 2 occurred during a single fall storm). Consequently, CPOM export-discharge relationships differed not only among streams but also between years and did not show treatment effects.

Treating C 54 with methoxychlor during Year 2 resulted in massive invertebrate drift and drastically reduced populations of macroinvertebrates, practically eliminating shredders and collector-filterers. Maximum discharge continued to be a good predictor of FPOM export ($r^2 = 0.83$) for C 54 during the treatment year, but the yield of export per unit of maximum discharge (slope of the discharge-FPOM export regression) decreased by 65%. This contrasts with the untreated streams in which the slopes were constant between years despite the >50 year drought during Year 2. Most (75%) of the decrease in FPOM yield from C 54 is directly attributable to the reduction in macroinvertebrates. Only 25% is attributable to the drought even though stream flows dropped by ca. 40% during Year 2.

Relationships between export and discharge observed in this study are stronger than those reported elsewhere because measurements of export were made independent of discharge over long time intervals (ca. 2 wk). Collecting export over 2-wk intervals clearly shows the effects of storms while avoiding the problem of hysteresis commonly seen in relationships between discharge and export concentration made during single storms.

Key words: particulate organic matter, export, discharge, streams, drought, invertebrate manipulation, insecticide, methoxychlor, Appalachian Mountains, USA.

Previous experiments in which macroinvertebrate communities have been manipulated with the insecticide methoxychlor (Wallace et al. 1982, Cuffney et al. 1984, Wallace et al. 1986, 1987) have shown that reducing the size of macroinvertebrate populations decreases both the rate of leaf litter processing and the concentration of FPOM exported relative to a nearby untreated stream. However, seston measurements in these studies were made using discontinuous grab sampling techniques and the relationship between discharge and export was not addressed (Cuffney and Wallace 1988). In this study, we expand upon our earlier work and separate physical and biological influences on long-term seston export by first establishing and comparing relationships between physical factors (maximum, minimum, total, and range of discharges in a sample interval) and export before and during treatment with methoxychlor.

To accomplish this, we had to independently measure the discharge parameter and export. Typically, export is estimated from instantaneous (discrete or grab) collections of concen-

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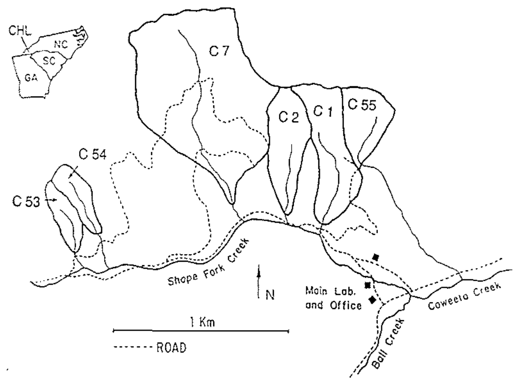

FIG. 1. Location of the Coweeta Hydrologic Laboratory, the three study streams draining Catchments 53, 54 and 55 and the stream (C 2) used to estimate winter discharges. Elevations (m asl) at gauging flumes are as follows: C 53 = 829; C 54 = 841; and, C 55 = 810.

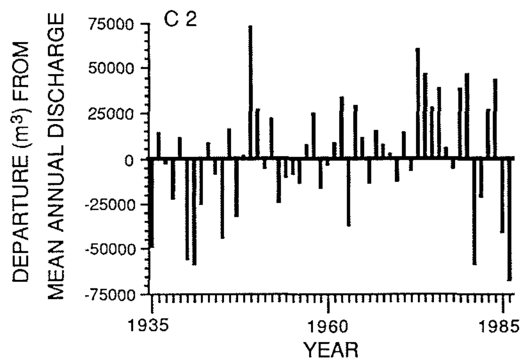

FIG. 2. Yearly departures from mean annual discharge (=96,424 m^3) for Catchment 2 at Coweeta for the period of 1935 to 1986. Note that 1986 was the worst drought on record.

tration (mg/L) multiplied by discharge. Export over longer time intervals, annual, is estimated by assuming that a predictive or consistent relationship exists between grab concentration and discharge. However, discharge typically explains <50% of the variability in POM concentration (Bormann et al. 1974, Cummins et al. 1983, Webster et al. 1987). Other predictors, such as stream power (Sedell et al. 1978), have been used to predict export concentrations but with mixed results (Fisher and Likens 1973, Meyer and Likens 1979, Webster and Patten 1979, Bilby and Likens 1979, Naiman and Sedell 1979, Naiman 1982, Webster et al. 1983).

Another problem associated with predicting POM concentration using discharge, or a parameter derived from discharge, is the phenomenon of hysteresis: POM concentrations measured at similar discharges are typically higher on the rising limb of a storm flow hydrograph than on the falling limb (Paustian and Bestcha 1979, Gurtz et al. 1980, Whitfield and Schreier 1981, Webster et al. 1983, Golladay et al. 1987, Webster et al. 1987). Webster et al. (1987) have shown a strong correlation between rate of change in discharge and seston concentration during rising but not falling hydrographs. Since the bulk of export during storms probably occurs on the rising hydrograph, when export concentrations are 10 to 50× baseflow concentrations (Gurtz et al. 1980, Webster et al. 1983, 1987, Golladay et al. 1987), then total export (g $storm^{-1}$) may be related to a discharge characteristic that predicts peak storm flow POM concentration.

We overcame problems of discontinuous export estimates and hysteresis by sampling export continuously over entire storms rather than discretely. Our objectives in this paper are to develop, for three small headwater streams, predictive relationships between POM export (CPOM and FPOM) and discharge characteristics (maximum, minimum, range, total, and average) using cumulative collections over relatively long intervals (2 wk) as individual samples. The relationships between discharge and export obtained during pretreatment and treatment periods are then compared to determine the relative importance of physical and biological components in controlling seston export.

Study Sites

The three streams studied (Fig. 1) are first-order headwater streams draining heavily forested catchments at the U.S. Forest Service Coweeta Hydrologic Laboratory (CHL), Macon County, North Carolina, USA. These streams are similar in size, aspect, elevation, gradient, thermal regime, and discharge (Cuffney and Wallace 1988). They are similar to other Coweeta streams in having low ion concentrations (<1 mg/L) and pHs of 6.6 to 6.8 (Swank and Waide 1987). Starting in 1985, the Coweeta Basin experienced drought conditions and in 1986 record low stream discharges were measured during the worst drought in >50 y (Fig. 2).

C 53 and C 54 were part of an earlier study in which C 53 was treated with an insecticide in 1980 (Wallace et al. 1982, Cuffney et al. 1984). By 1985, C 53 had a diverse assemblage of macroinvertebrates and all taxa present in the drift during the initial treatment in 1980 were recovered from monthly benthic samples (J. B. Wallace, unpublished data). C 54 was similarly treated in December of 1985. Additional site descriptions for these streams can be found in Wallace et al. (1982, 1986, 1987), Cuffney et al. (1984), and Cuffney and Wallace (1988).

Methods

Methoxychlor treatments and macroinvertebrate communities

C 54 was treated with the insecticide methoxychlor (1,1,1-tri-chloro-2,2-bis[p-methoxyphenyl]ethane; CAS No. 72-43-5) seasonally beginning on 10 December 1985. Methoxychlor was initially applied, using hand sprayers, along the entire stream at a rate of 10 ppm for 4 hr based on discharge at the flume. Shorter (ca. 2-hr) 10 ppm treatments were repeated at ca. 3-mo intervals. Additional details of treatments, concentrations of methoxychlor in stream water, residues in stream sediments, and effects of treatment on benthic animals and drift are reviewed in Wallace et al. (1989).

Benthic organisms were collected from red maple and rhododendron leaf litter bags using techniques described by Wallace et al. (1986). Leaf bags were placed in the streams on 12 December 1984 and again on 12 December 1985, immediately following treatment of C 54. Leaf bags were retrieved at similar intervals over the course of each year. Density and functional groups of animals colonizing leafbags were compared over equivalent pre-treatment and treatment periods.

Discharge

Stream flow was gauged continuously during non-freezing months (April through November) using FW-1 stage recorders attached to a 1-ft H-flume (Agricultural Research Service 1962) (Cuffney and Wallace 1988). Stage/discharge relationships were derived for each stream from field measurements of stage and discharge. Discharge relationships between a continuously gauged stream, C 2 (Fig. 1), and the study streams were used to estimate discharge during freezing months (December through March). Instantaneous measurements of discharge (stage height in flumes checked during winter months) were strongly related to discharge in C 2 ($r^2 = >0.95$). Recurrence intervals of storm discharges were calculated using the methods of Leopold et al. (1964).

Export estimates

FPOM export was collected continuously using a Coshocton wheel proportional runoff sampler (Parsons 1954) mounted below the H-flume. The Coshocton subsampler delivered 0.6% of stream flow into a sequence of three covered 125-L settling barrels. These barrels removed a constant proportion (85%) of FPOM (Cuffney and Wallace 1988). Barrels were sampled and cleaned at weekly (10 December 1984 to 14 May 1985) or biweekly (14 May 1985 to 28 March 1987) intervals. With one exception, stream discharge had returned to near baseflow conditions by the time of barrel sampling and no samples were collected during rising storm hydrographs. The total FPOM export (Expt) during each collection interval was then calculated as:

$$\text{Expt} = B_t/(E_f \times C_s)$$

where B_t is the amount (g ash free dry mass [AFDM]) recovered from the three barrels, E_f is the export barrel extraction efficiency (0.85), and C_s is the proportion of discharge sampled by the Coshocton subsampler (0.006). This method of continuously measuring FPOM export is described in Cuffney and Wallace (1988). All POM samples were dried (60°C for 5 d), weighed, ashed (500°C for 1–4 hr), and reweighed to determine AFDM.

CPOM export was collected continuously using a rectangular cage (ca. 3 m long, 2 m wide, 1 m high) constructed of galvanized hardware cloth (mesh = 4 × 4 mm) attached to a wood frame. The upstream end of each trap was bolted to the base of a high gradient rock outcrop 2–10 m above the H-flume. Even during extreme discharges, the traps sampled the entire stream flow and their large size prevented accumulated material from being processed to smaller particles as a result of exposure to high water velocities. Each trap was covered with a plastic canopy to exclude litterfall. The contents of traps were removed at 2-wk intervals and separated into two size classes, ≥4 mm and <4 mm. The material <4 mm was added to the estimate of FPOM export. Material ≥4 mm was sorted into three categories: leaves, wood, and other. Usually, the entire contents of each trap were collected and quantified. However, on 26 November 1986 it was necessary to subsample because of the large volume of material in the traps. This was accomplished by measuring total wet weight in the field using a bucket and spring balance. A representative subsample was weighed in the field and returned to the laboratory for processing.

Discharge versus export relationships

The relationships between discharge and export were investigated using linear regression. Regressions were used to relate one of five discharge parameters (independent variable = maximum, minimum, range, total or average discharge) to total export of either CPOM (total, leaf or wood) or FPOM. Relationships between discharge and export were compared between years and between streams to determine the effect of the drought on export of POM. Regressions were forced through the origin to meet the a priori requirement that export ceased if there was no discharge.

Separation of physical and biological factors controlling export

The record drought of Year 2 presented the opportunity to separate changes in C 54 export due to physical (drought) and biological (benthic community alteration) changes. To accomplish this, discharge-export regressions obtained before treatment (Year 1) were coupled with discharge measurements made during Year 2 to obtain an estimate of export expected during Year 2 in the absence of treatment effects. This method assumes that the slopes of discharge-export relationships do not differ significantly among years in the reference streams (see below). Changes in export due to drought and treatment are then calculated by difference:

(1) Effect due to drought and treatment = A − B
(2) Effect due to drought = A − C
(3) Effect due to treatment = C − B

where A is the pretreatment export (Year 1), B is the treatment export (Year 2) and C is the predicted export during Year 2.

Results

Effects of methoxychlor on C 54 benthos

Densities of shredder and collector-filterer functional groups were reduced by 94% and 99%, respectively, in post-treatment (January 1986) benthic samples compared to pre-treatment samples (November 1985) (Wallace et al. 1989). Collections during subsequent methoxychlor treatments indicated that these changes in community structure persisted throughout the second year of this study (Wallace et al. 1989, unpublished data).

Densities of shredders associated with leafbags

Shredder abundance in red maple and rhododendron leafbags were not significantly different among the streams prior to treatment (Fig. 3). Common shredders included species of Plecoptera (*Leuctra*, Peltoperlidae, Nemouridae), Trichoptera (*Pycnopsyche, Lepidostoma, Fattigia*), Diptera (*Tipula*) and Decapoda (*Cambarus*). Virtually all these taxa, with the exception of some tipulids, were eliminated by the methoxychlor treatments. Consequently, 95% CLs of shredder density in C 54 did not overlap with those of C 53 and C 55 during the treatment year, indicating significant reduction had occurred (Fig. 3). Densities in C 53 and C 55, however, did not differ significantly between the two years despite the drought during the second year.

Physical control of FPOM export

Only two discharge parameters (maximum and range) were significantly correlated (r = 0.82 to 0.99) with FPOM export in the study streams. Discharge range, which was used to characterize the magnitude of storms during sample collection intervals, was highly correlated with maximum discharge ($r \geq 0.99$, Table 1) and had no value as an independent estimator. Consequently, all export relationships were developed using maximum discharge.

Export values of FPOM per unit maximum discharge (slope of linear regressions through the origin) from C 53 and C 55 (Table 2) were

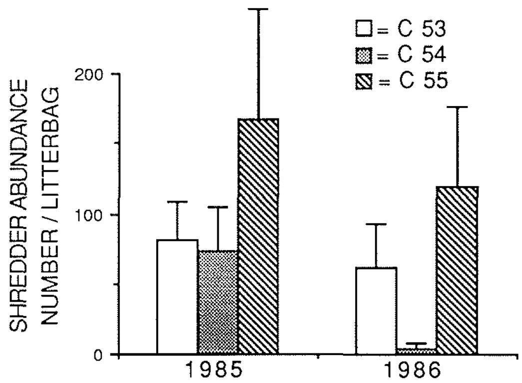

FIG. 3. Mean number of shredders per litterbag (+95% CL) in streams draining C 53, C 54, and C 55 during January through May 1985 and the same period of 1986 (pre-treatment vs. treatment year for C 54).

not significantly different from one another during either year, though the export for C 54 was significantly ($p < 0.05$) different from both C 53 and C 55 in both years (analysis of covariance, Newman-Keuls multiple range test [Zar 1984]). Comparisons of FPOM export versus maximum discharge relationships among years show that relationships obtained from untreated streams did not differ significantly among years ($p > 0.05$, F test for coincidental regression [Zar 1984]) despite the record drought during Year 2 (Fig. 2). However, methoxychlor treatment of C 54 during Year 2 drastically changed the relationship between maximum discharge and FPOM export, reducing the yield of FPOM per unit of maximum discharge by 65%.

The hydrologic regime of the three streams differed between the two years as a result of the continuing drought. Base flow discharges tended to decrease through time as the drought continued (Figs. 4a, b) and total annual discharge decreased in the year of the record drought (Year 2). In addition, the number of large storms (>4 L/s maximum discharge) and small (<4 > 2 L/s maximum discharge) storms decreased during Year 2 (large storms: Yr 1 = 7, Yr 2 = 4; small storms: Yr 1 = 16, Yr 2 = 9). The time between storms increased and general intensity of storms decreased. Despite these differences, FPOM discharge relationships for untreated streams during Years 1 and 2 were similar indicating the same mechanisms were in operation (Fig. 5).

TABLE 1. Correlations among discharge variables measured in C 53, C 54 and C 55. Data are for the period 10 December 1984 to 7 December 1986 ($p < 0.05$ for $r > 0.259$). C 54 was the treated stream starting in December 1985.

	Catchment 53				Catchment 54				Catchment 55			
	Minimum	Range	Total	Average	Minimum	Range	Total	Average	Minimum	Range	Total	Average
Maximum	−0.0735	0.9969	0.4106	0.1776	−0.0232	0.9947	0.2967	0.1373	−0.0181	0.9941	0.4146	0.2308
Minimum		−0.1518	0.6382	0.9300		−0.1257	0.6384	0.8969		−0.1268	0.6892	0.8861
Range			0.3565	0.1025			0.2289	0.0442			0.3364	0.1326
Total				0.8272				0.8237				0.8809

TABLE 2. Maximum discharge-FPOM export relationships used to separate drought and treatment effects. Curves are linear regressions through the origin using maximum discharge (X) and g AFDM of FPOM exported during collection interval (see Cuffney and Wallace 1988) ($p < 0.001$ for all regressions). C 54 was the treated stream in 1986.

	C 53		C 54*		C 55	
	1985	1986	1985	1986	1985	1986
Slope	359.9	395.8	678.6	238.1	428.0	452.1
SE	22.6	10.5	42.0	16.6	29.4	21.5
r^2	0.75	0.98	0.76	0.83	0.70	0.92
n	30	26	30	26	30	26

* Slopes are significantly different ($p < 0.05$) between years.

Physical control of CPOM export

CPOM export (total, leaf and wood) correlated well with maximum discharge and discharge range but not with average, total, or mean discharge. However, for CPOM regressions (Table 3), the relationships were not as strong (r^2 = 0.48 to 0.80) as for FPOM. CPOM was severely influenced by storms, particularly one that occurred soon after peak litterfall during Year 2 (26 November 1986). This was the most intense storm encountered during the study. Discharge rose from <1 L/s to >22 L/s in 12 hr and resulted in 78–88% of total annual CPOM export and 25–33% of annual FPOM export during Year 2 (Table 4). The storm strongly influenced the relationship between discharge and CPOM export. For example, the significant relationship of leaf and total CPOM with maximum discharge from C 53 during Year 2 breaks down entirely when the storm is excluded (r^2 falls from ca. ≥0.79 to <0.2). The storm of 26 November 1986, which was so important in determining annual export of CPOM and FPOM, is not atypical or rare for these streams. Maximum discharges observed during Year 1 (12.9 L/s) and Year 2 (22.8 L/s) represent storm flows which have recurrence intervals of 1.2 and 1.8 years, respectively. Consequently, we can expect that more intense storms with longer recurrence intervals (10 yr and 20 yr storms) would have an even greater impact upon annual CPOM export.

Unlike FPOM, there are significant differences in CPOM discharge-export relationships between years when the storm of 26 November 1986 is included in the analyses (i.e., higher CPOM export per unit maximum discharge during Year 2). CPOM export relationships are much more similar between years when the November 1986 storm is not included in the analyses. However, factors other than discharge are also important in controlling CPOM export and the importance of these factors changed between the two years of this study.

Physical versus biological control of export

The relationships between CPOM export and discharge were not consistent between years for C 53 and C 55. Therefore, we could not assume that the discharge-CPOM export relationship observed in C 54 during the pretreatment year would have been applicable to the following year in the absence of treatment. Consequently, a predicted treatment CPOM export could not be calculated, and drought and treatment effects could not be separated.

Discharge-FPOM export relationships were consistent between years for C 53 and C 55, and we were able to separate drought and treatment effects for FPOM in C 54 (Fig. 6). The combined effects of drought and treatment reduced FPOM export by 66.7% compared with export during the previous year. Drought accounted for ca. 25% of this reduction whereas manipulation of the invertebrate populations accounted for ca. 75% of this difference.

DISCUSSION

Influence of methoxychlor on benthic communities

The shift in the structure of the benthic community from large macroinvertebrates (e.g., stoneflies, caddisflies and crayfish) to a com-

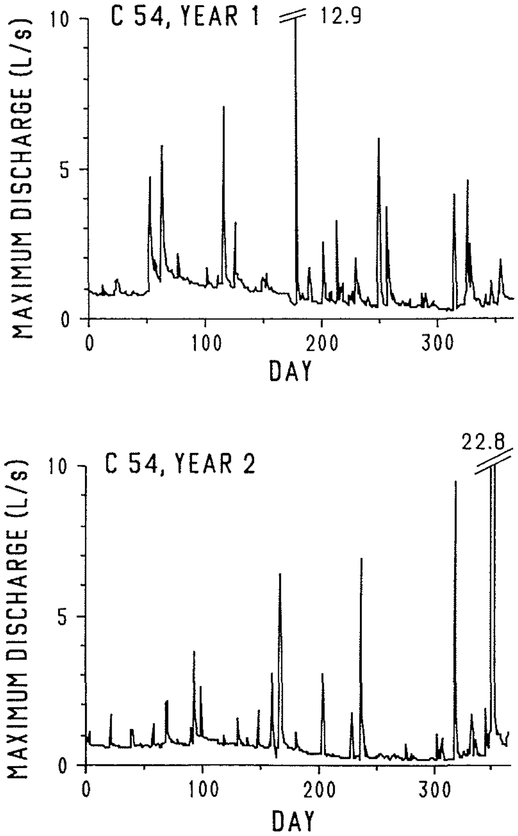

FIG. 4. a and b. Hydrographs for C 54 during Year 1 (top) and Year 2 (bottom) based on maximum daily discharge.

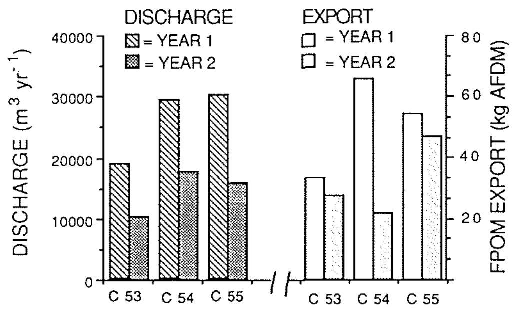

FIG. 5. Total discharge and total FPOM export during Year 1 and Year 2 (record drought year and treatment year [C 54]). Note that per m^3 of discharge much less FPOM was exported from C 54 during the treatment year.

munity dominated by small invertebrates (e.g., chironomids, Turbellaria, Oligochaeta, Copepoda) and a few large insect predators (see Wallace et al. 1989) also represented a drastic alteration of the functional characteristics of C 54. Reductions in densities in C 54 were evident by comparing pre-treatment vs. treatment samples (Wallace et al. 1989) and in comparisons with the reference stream (C 55) and C 53 (J. B. Wallace, unpublished data). The communities in C 53 and C 55 did not change dramatically from year to year, establishing that changes observed in C 54 community structure, particularly shredder densities, were due to insecticide treatment and not drought. All our invertebrate data suggest that treatment of C 54 successfully reduced shredders, which are theoretically the most important functional group in producing FPOM from CPOM. Alterations of community structure reported here were similar to results obtained when C 53 was treated with methoxychlor in 1980-81 (Cuffney et al. 1984, Wallace et al. 1982, 1986).

Physical control of FPOM export

Our discharge-export regressions show that FPOM export is directly controlled by maximum discharge during the sampling interval. The observed discharge-export relationships in the untreated streams are relatively simple (fitted well by linear models), not significantly different from year to year, not significantly affected by severe drought, and far stronger than relationships reported elsewhere between discharge and export concentration (mg/L) from grab samples (Cummins et al. 1983). The strong discharge-FPOM export relationships obtained in this study are attributable to the use of separate gauging flumes and export samplers which sampled export continuously over relatively long time intervals (ca. two weeks). These devices allowed independent measurements of export and discharge for each sample interval and permitted comparisons of discharge-export relationships in a statistically legitimate manner. In contrast, there are many examples in the literature that compare FPOM export, obtained from grab concentrations (i.e., concentration × discharge = export), to discharge or to a variable related to discharge (e.g., stream order, basin area). Such studies report significant relationships that may be due to autocorrelation rather than cause and effect.

The 2-wk cumulative sampling interval also

TABLE 3. Linear regressions through the origin which relate maximum discharge (L/s) and CPOM (leaf, wood and total) export (g AFDM) in a sample collection interval ($p < 0.002$, for all regressions). Year 1 is the period 10 December 1984 to 7 December 1985, Year 2 is from 7 December 1985 to 10 December 1986. C 54 was the treatment stream during Year 2.

	C 53		C 54		C 55	
	Year 1	Year 2	Year 1	Year 2	Year 1	Year 2
Leaf						
Slope	10.48	93.71	27.12	220.65	13.86	88.86
SE	1.86	9.32	2.70	27.56	1.79	13.98
r^2	0.48	0.79	0.73	0.70	0.55	0.59
n	24	26	24	26	24	26
Wood						
Slope	9.31	61.59	13.72	118.86	16.86	107.22
SE	1.17	5.94	1.90	15.14	2.35	17.20
r^2	0.69	0.80	0.63	0.70	0.56	0.57
n	24	26	24	26	24	26
Total CPOM						
Slope	25.23	202.83	45.11	408.30	38.67	238.89
SE	3.40	19.84	4.48	51.18	4.37	36.24
r^2	0.64	0.80	0.74	0.70	0.64	0.61
n	24	26	24	26	24	26

avoided complications associated with the phenomenon of hysteresis, i.e., disparate POM concentrations observed at similar discharges on the ascending and descending limbs of a storm hydrograph (Webster et al. 1987). The sampling interval was longer than individual storms (Figs. 4a, b), ensuring comparisons of discharge and export from one or more complete storms rather than portions of a storm. By expanding the temporal scale of sampling, the effect of hysteresis was avoided and the relationships between discharge and export greatly simplified.

The record drought of Year 2, which represented a 50+ year drought (Fig. 2), presented a unique opportunity to examine the effect of physical changes on FPOM export. The total amount of FPOM exported was reduced in Year 2 in the untreated streams and during both years sampling intervals containing storms of equal intensity (equal maximum discharges) resulted in similar export (similar slopes for maximum discharge-FPOM export, Table 2) despite differences in the time between storms, storm frequency or intensity between years (cf. Figs. 4a, b). This conclusion applies to data collected during two years which are known to be well below the mean annual discharge for the area (Fig. 2). Additional long-term data (e.g., >5 yr), encompassing both normal and wet years, will be necessary to provide a more inclusive and comprehensive model of the relationship between discharge and FPOM export for these streams. Furthermore, acquisition of such long-term data may provide insight into potential seasonal differences in maximum discharge-export relationships and allow comparison of these streams to other geographical areas with different sized streams and storm hydrographs (less quick flow).

The proportion of FPOM export that occurred during sampling intervals containing a storm actually increased during the severe drought (Year 2) though storms were less frequent (Cuffney and Wallace 1988). Furthermore, reductions in FPOM export during the drought (C 53, 16.4%; C 55, 13.1%) were more similar to the reduction in annual precipitation (18.4%) than to the reduction in annual stream discharge (C 53, 44.9%; C 55, 47.1%). These results emphasize the importance of storms in export dynamics of high gradient headwater streams. These streams respond rapidly to storms, producing intense but brief discharge peaks (Figs. 4a, b). However, they spend most time at or near baseflow, as evidenced by the high degree of correlation between total discharge and minimum discharge (Table 1). Storm-related discharge peaks

TABLE 4. Organic matter export (kg AFDM) from study streams during 1985 and 1986. Values in parentheses are the percentage of annual export during Year 2 that occurred during the storm of 26 November 1986 (Storm). C 54 was the treatment stream in 1986.

		1985	1986	Storm
C 53	FPOM	33.27	27.83	9.25 (33.2%)
	CPOM	1.23	6.58	5.81 (88.3%)
C 54	FPOM	65.63	21.83	5.34 (24.5%)
	CPOM	2.64	15.48	13.34 (86.2%)
C 55	FPOM	54.24	47.12	11.55 (24.5%)
	CPOM	4.78	12.56	9.58 (78.4%)

are the predominant mechanism by which FPOM is exported.

Physical control of CPOM export

Other studies have suggested that peak discharge, interval between storms, storm sequence, time of year, amount of litterfall, and decomposition rates of POM must be considered for an adequate definition of the CPOM export-discharge relationship even for a single stream (Cummins et al. 1983). Although these factors were not necessary for our FPOM export-discharge relationships, they are relevant for CPOM relationships, which were much more variable and showed seasonal effects. CPOM export is strongly influenced by the seasonality of inputs (>75% of CPOM enters these streams during autumn litterfall, J. B. Wallace, unpublished data) and the rate at which CPOM is processed (the bulk of litterfall, leaves, is processed in ca. 6–9 mo, Cuffney et al. 1989). Thus, leaf availability is highly seasonal and storms that occur when the standing crop of leaves is greatest (autumn, early winter) will result in maximum export of CPOM. This explains much of the seasonality observed in our CPOM export samples and why export was actually higher during the drought year (the intense storm of 26 November 1986) than during the previous year.

In contrast, FPOM is in relatively constant supply throughout the year because the large quantities of FPOM stored in benthic sediments (ca. 420–530 g AFDM/m^2, J. B. Wallace, unpublished data) are augmented by FPOM formed by the processing of leaves (ca. 500 g m^{-2} $year^{-1}$, J. B. Wallace, unpublished data). Consequently, the supply of FPOM is much more stable than CPOM, and discharge-FPOM export relationships are less variable and lack the seasonal influences displayed by CPOM.

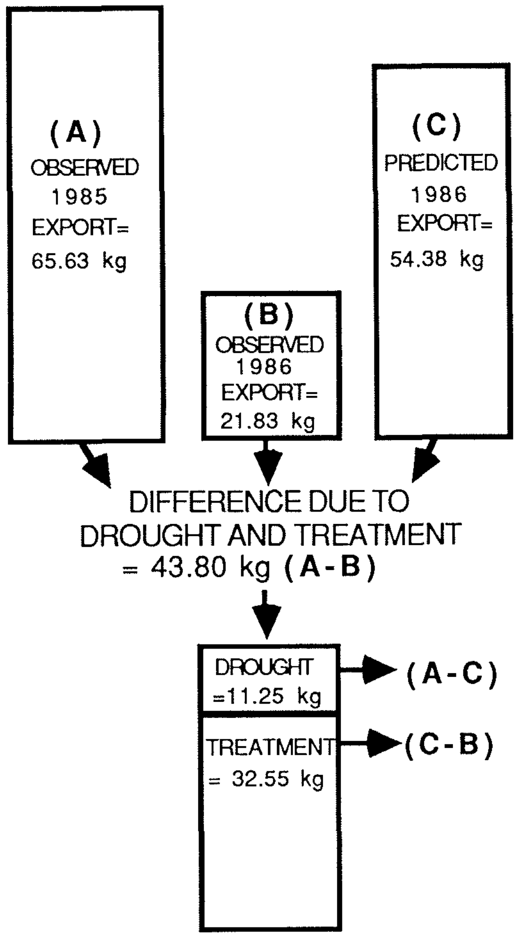

FIG. 6. Procedure for calculating drought and manipulation effects for FPOM export from C 54. Exports from 1985 (A = pretreatment year) and 1986 (B = treatment year) are measured parameters. Predicted 1986 export (C) is based on the 1985 relationship between maximum discharge and the amount of FPOM exported.

Physical versus biological control of FPOM export

C 54 showed the only discharge-export regression that changed significantly between years, strongly implying that reducing the macroinvertebrate populations had a significant impact upon FPOM export (Fig. 6). Relative to the record drought effect, the magnitude of the treatment effect showed that drought accounted for only ca. 26% (11.25 kg AFDM) whereas invertebrate manipulation accounted for almost 75% of the observed reduction in FPOM export. Therefore, reducing the invertebrate community decreased FPOM export by about three times that of a >50-yr drought. These differences cannot be attributable to microbial processes, as treatment of C 54 did not alter microbial respiration in benthic, leaf, or woody litter samples relative to C 53 or C 55 (Cuffney et al., 1989).

Although the slope of the discharge-FPOM export regression changed as result of treatment of C 54, maximum discharge remained an effective predictor of FPOM export. This implies that the mechanism by which FPOM is transported during storms remained the same in the treated stream but that the reservoir of transportable FPOM decreased. Reasons for the decrease could be: (1) significant reductions in the total standing crop of FPOM, (2) reduction in the amount of "new" FPOM generated by shredding, (3) reduction in the amount of loose surface FPOM generated by movements and feeding activities of macroinvertebrates, and (4) greater retention of FPOM by accumulating leaf litter within the stream bed, as a result of lower leaf processing rates (Wallace et al. 1982, and J. B. Wallace, unpublished data) in the treated stream (e.g., Short and Ward 1981).

Standing crop of FPOM did not differ significantly in C 54 between Year 1 and Year 2 (standing crop of FPOM increased slightly in Year 2, J. B. Wallace, unpublished data). Lack of shredder-generated FPOM and fewer active macroinvertebrates appear to be the more probable mechanisms for reduction in transportable FPOM because both would have occurred shortly after application of methoxychlor. This would explain the abrupt change in discharge-export relations observed between treated and untreated periods. Conversely, if there was a gradual exhaustion of stored FPOM during the treatment period, or increased retention by unprocessed leaf material, the yield of FPOM per unit of maximum discharge should continue to decrease with time. The reservoir of stored FPOM is very large relative to the amount exported annually. For example, minimum estimates of stored FPOM (wetted perimeter measured during severe drought conditions) indicates that FPOM storage exceeds export by 1.2 to 3.7 fold. When bankful storage and annual processing of CPOM to FPOM are included in the estimates, then storage greatly exceeds export (J. B. Wallace, unpublished data). Although this FPOM is probably not all equally exportable, significant reductions in total standing stock of FPOM would not occur for some years after treatment even if all FPOM inputs ceased. Consequently, feeding (e.g., shredders, collectors, etc.) and movements of macroinvertebrates appear to be responsible for the observed reductions in FPOM export between treated and untreated years. It is impossible to separate the contributions of shredding from those of other feeding modes or movements of invertebrates without detailed information on CPOM inputs and processing rates, and export and storage of CPOM and FPOM. The analyses of organic matter budgets between years and among treated and untreated streams will be examined in a subsequent paper.

Acknowledgements

A. Lingle, F. Smith-Cuffney, P. Egens, G. Schurr, G. J. Lugthart and D. Imm assisted with laboratory and field work. Ms. B. S. Goldowitz, Drs. A. D. Huryn, Rosemary Mackay, Pat Mulholland, and two anonymous reviewers provided critical comments on earlier drafts of the manuscript. This research was supported by grants BSR83-16082 and BSR87-18005 from the National Science Foundation.

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Received: 7 February 1989
Accepted: 22 August 1989